

RELATIONAL LEARNING IN A CONTEXT OF TRANSPOSITION: A REVIEW

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In a typical transposition task, an animal is presented with a single pair of stimuli (for example, S3+S4−, where plus and minus denote reward and nonreward and digits denote stimulus location on a sensory dimension such as size). Subsequently, an animal is presented with a testing pair that contains a previously reinforced or nonreinforced stimulus and a novel stimulus (for example, S2−S3 and S4−S5). Does the choice of a novel S2 instead of previously reinforced S3 in a testing pair S2−S3 indicate that the animal has learned a relation (i.e., “select smaller”)? This review of empirical evidence and theoretical accounts shows that an organism’s behavior in a transposition task is undoubtedly influenced by prior reinforcement history of the training stimuli (Spence, 1937). However, it is also affected by two other factors that are relational in nature—a similarity of two testing stimuli to each other and an overall similarity of the testing pair as a whole to the training pair as a whole. The influence of the two latter factors is especially evident in studies that use multiple pairs of training stimuli and a wide range of testing pairs comprising nonadjacent stimuli (Lazareva, Miner, Young, & Wasserman, 2008; Lazareva, Wasserman, & Young, 2005). In sum, the evidence suggests that both prior reinforcement history and relational information affect an animal’s behavior in a typical transposition task.

Key words: transposition, stimulus discrimination, relational learning, generalization, multiple pair training, review

Relational learning, an ability to recognize and respond to relationship among objects irrespective of the nature of those objects, has long been recognized as a hallmark of human reasoning. As C. Lloyd Morgan eloquently stated in his *Introduction to Comparative Psychology*,

...[I]n comparing the psychology of man and the higher animals, the radical difference lies in the fact that man perceives particular relations among phenomena, and builds the generalized results of these perceptions into the fabric of his conceptual thoughts; while animals do not perceive the relations, and have no conceptual thought, nor any knowledge—if we use this word to denote the result of such conceptual thought.

(Lloyd Morgan, 1903, pp. 362–363)

Can animals respond to the relations between objects? Although many experimental approaches addressing this question exist, one of the first attempts to examine relational learning in a nonhuman organism was made

by Köhler (1918/1938). In a first series of Köhler’s experiments, chickens were presented with a simple simultaneous discrimination in which a response to a darker shade of grey was not reinforced and a response to a lighter shade of grey was reinforced (or vice versa). Once the chickens learned the original discrimination, they were given a choice between the original lighter shade of grey and a novel, still lighter, shade of grey. Köhler reasoned that if the chickens learned to respond to a specific shade value, then they ought to select the original grey shade given in training; but, if they learned to respond to the lighter of two shades (i.e., to the relationship between the two shades), then they ought to respond to the novel shade and ignore the previously reinforced shade. Köhler reported that chickens (and, in the subsequent experiments, apes) selected the novel shade on over 70% of trials, indicating a preference for “relationally correct” stimulus. Köhler called this behavioral result transposition—just as the notes of musical melodies do not change their relation to each other when the melodies are moved or transposed to different keys, the learned relation remains intact when new stimuli are substituted.

DESIGN OF A TYPICAL TRANSPOSITION EXPERIMENT

Most of transposition research has used a single-pair, two-stimulus design summarized in

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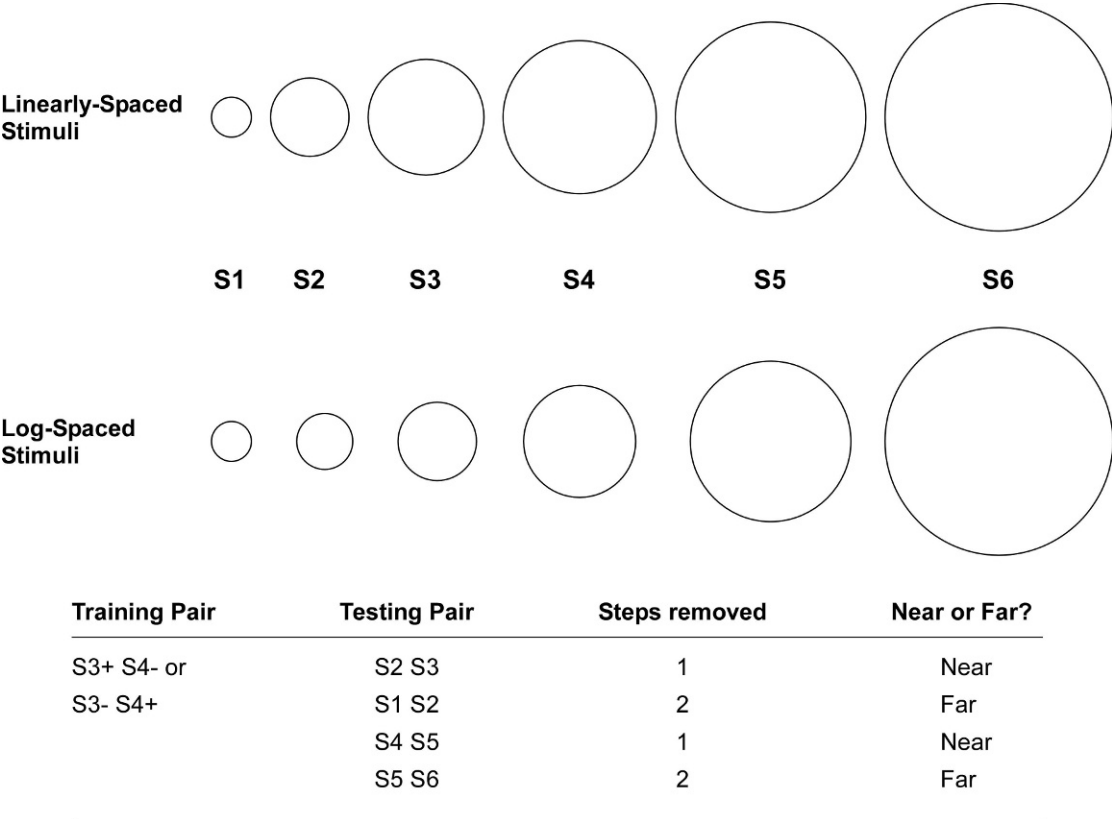


Fig. 1. Schematic depiction of typical transposition design and related terminology. See text for details.

Figure 1. In this design, a subject is given a single pair of training stimuli (e.g., S3+ S4−, where numbers stand for stimuli and plus and minus indicate reinforcement or nonreinforcement), and is then presented with testing pairs composed of adjacent stimuli that are progressively removed from the training pairs. The pair S4–S5 is said to be one step removed from the training pair and is usually termed a *near test pair*. The pairs that are two or more steps removed from the training pair are termed *far test pairs*.

Another critical feature of transposition design is the spacing of the stimuli along a sensory dimension. As Figure 1 illustrates, the stimuli can be spaced either *linearly* using equal increments from one stimulus to another, or *logarithmically* using equal ratios of one stimulus to the next stimulus. In his seminal paper, Spence (1937) argued that the stimuli need to be spaced “in line with the Weber–Fechner relation between sensory and stimulus dimension” (p. 434), or logarithmically. Later

theoretical research showed that spacing of the stimuli along a dimension is indeed critical for predicting choices in a transposition test (see Rilling, 1977, for a review). Most of the transposition research has used logarithmic spacing of the stimuli, and a few studies employing linear spacing of the stimuli implemented logarithmic transformation of stimulus values for plotting the gradients and predicting test choices (Lazareva et al., 2005; 2008).

Relational learning has also been studied using the intermediate stimulus problem design. In these experiments, subjects were presented with the three (instead of the two) stimuli and trained to select the middle stimulus (e.g., stimulus S3 in a trio S2–S3–S4). Although this design has produced data challenging Spence’s stimulus discrimination theory, it has received considerably less attention than the traditional two-stimulus transposition design and will not be reviewed here (see Reese, 1968; Riley, 1968, for detailed reviews).

HOW TO INTERPRET CHOICES IN A TRANSPOSITION EXPERIMENT

Köhler's Relational Account

Köhler (1918/1938) summarized the essential points of his relational account of transposition along the dimension in the following manner:

(a) The individual colours appearing in a pair attain an inner union [T]heir role in this union depends ... upon their places in the system they compose. (b) If their places with respect to each other are held constant but a variation is made in their absolute quality, ... the perceived relationship will be transposed. ... [T]he essential characteristic of togetherness has not been changed by this transposition: both cases are two-colour wholes; both allow the same judgment of "one colour brighter than the other".

The "inner union" in both Gestalt- and relation-perception depends in either case upon a common basic function..., the term referring to that feature of a perceived Gestalt or a perceived relation which is *common* to both. Differences between them here are intentionally ignored. (p. 221)

This position implies that an organism does not need to directly perceive a relation in order to exhibit transposition. Instead, a configuration of discriminative stimuli can be perceived holistically, and, if this whole is unchanged, then the change in the absolute values of the stimuli does not affect responses (see also Gulliksen & Woffle, 1938; Klüver, 1933; Stevenson & Bitterman, 1955). In later work, Köhler (1929) also suggested that an organism may be learning both absolute properties of the stimuli and the relationships among them, but retaining relational information longer. Finally, Köhler has proposed that simultaneous presentation of the stimuli ought to be critical for observing transposition since unlike successive presentation it allows for a direct comparison among the stimuli. However, relational accounts advanced by Köhler and other theorists tended to provide a posteriori explanations for new experimental findings instead of a priori predictions that could be verified empirically (see Reese, 1968, for a review).

Spence's Discrimination Theory

Does a seemingly relational choice in transposition design necessarily indicate relational

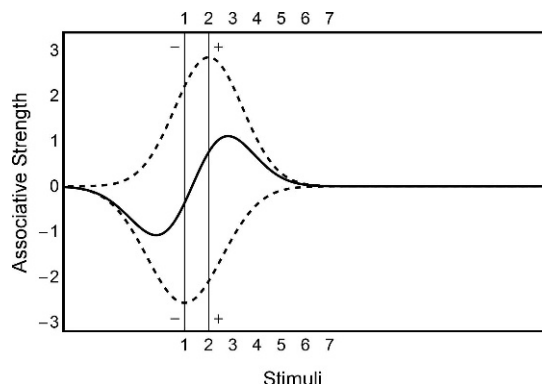


Fig. 2. Hypothetical excitatory and inhibitory gradients (dashed lines) and postdiscrimination generalization gradient (full line) illustrating predictions of Spence's (1937) discrimination theory after training with an S2+S1- discrimination. Vertical lines illustrate the location of previously reinforced and previously nonreinforced stimuli. Note that the postdiscrimination generalization gradient indicates "relational" choice in a pair S2-S3, "absolute" choice or transposition reversal in pairs S3-S4 and S4-S5, and a chance level performance in a pair S6-S7.

learning? A theoretical account proposed by Kenneth W. Spence (1937) suggested that a preference for a "relationally correct" stimulus in a transposition experiment could be explained without hypothesizing that animals actually perceive the relations between or among stimuli. Spence's discrimination theory is based on three simple premises illustrated in Figure 2. Firstly, there is a gradient of excitation (indicated by the dashed line) around a stimulus associated with reinforcement (or S+, which is S2 in this example), with a gradual decrease in excitation as stimuli are increasingly removed from it. Secondly, there is a similar gradient of inhibition (also indicated by a dashed line) around a stimulus associated with nonreinforcement (or S-, which is S1 in this example). Finally, when the S+ and the S- are located on the same stimulus dimension, the gradients of excitation and inhibition are summed, resulting in a postdiscrimination generalization gradient (or PDG; depicted by the solid line). The PDG determines the subject's response: The higher the net associative value of one stimulus, the greater the organism's preference for that stimulus in a choice test.

As Spence (1937) pointed out, the algebraic summation of excitatory and inhibitory gradients leads to a *peak shift*—a shift in the peak of

the net associative value from the S+ to the novel stimulus, or away from S- (e.g., a shift from S2 toward S3 in Figure 2). Thus, an organism may respond more to the novel stimulus than to the previously reinforced stimulus because the novel stimulus does, in fact, have a higher net associative value. Spence further noticed that as the stimuli become more removed from the original S+, the PDG predicts "absolute" choice or transposition reversal in certain pairs (e.g., S3-S4 in Figure 2) and chance responding in others (e.g., S4-S5 in Figure 2).

Unlike Köhler's (1918/1938) relational account, the rich predictions of Spence's (1937) theory generated a large body of research (see Reese, 1968; Riley, 1968, for detailed reviews). Empirical research confirmed that the overall shape of the *predicted* PDG, calculated as an algebraic sum of experimentally obtained excitatory and inhibitory gradients, is consistent with the shape of *experimentally* obtained PDG (Hearst, 1969; Honig, 1962; Marsh, 1972). Moreover, the empirical PDG was found to produce the peak shift predicted by Spence, and to provide reasonably accurate predictions for choice preference (Hanson, 1959; Honig, 1962; Honig & Urcuioli, 1981).

In a representative study, Honig (1962) trained pigeons to peck a key illuminated by a 550 nm light and refrain from pecking the key illuminated by a 560 nm light in a successive discrimination. Following this training, pigeons were given an opportunity to respond to a single stimulus varying from 490 nm to 620 nm. Later, they were presented with a choice between two simultaneously shown adjacent stimuli (e.g., 490 vs. 510 nm, 510 vs. 520 nm, and so on). Figure 3 depicts the results of this experiment. (The bars in this figure show number of responses to the two adjacent stimuli—for example, the black bar above 490 represents the number of choices to the 490 nm stimulus and the white bar next to it shows the number of choices to the 510 nm stimulus.) The PDG clearly showed a positive peak shift (solid line) from S+ (550 nm). The results from the simultaneous choice tests (black and white bars) showed a strong preference for a "relationally correct" stimulus when 540 and 550 nm were paired. As the stimuli moved farther away from S+, the birds responded primarily to the "relationally incorrect" stimulus. Still farther, this "absolute"

preference begins to decline toward chance level, providing a striking confirmation for Spence's (1937) theory.

Some experimental evidence, however, appeared to be at odds with Spence's (1937) account of transposition. First, Spence's theory assumes that simultaneous training and successive training are essentially equivalent and ought to produce comparable transposition. Yet, multiple studies have shown stronger transposition after simultaneous training than after successive training (Marsh, 1967; Riley, Ring, & James, 1960; but see Hebert & Krantz, 1965; Wills & Mackintosh, 1999). Spence's theory also cannot readily account for relational choices in an intermediate size problem (see Riley, 1968, for a review) or after discrimination training with multiple pairs of stimuli (as discussed below). Still, the precise nature of Spence's theory and its ability to generate many testable predictions was clearly preferred by many researchers to the ambiguous statements that characterized Köhler's (1918/1938) and other Gestalt theorists' accounts. As Spearman (1937) argued, the concepts proposed by Gestalt theorists "...are so vague that—like the ancient oracles—anything can be read into them; nothing read out of them" (p. 383; see also Reese, 1968, pp. 232–238, for a detailed depiction of the debate).

What Do We Know About Gradients?

When Spence (1937) proposed his account of transposition, the gradients he chose were arbitrary, "as little experimental evidence bearing on the problem is available" (p. 434). Later, extensive experimental research demonstrated that both excitatory and inhibitory gradients are largely symmetrical, with a maximum (or minimum) of responses centered at S+ (or S-). These gradients tend to be broad at the beginning of the training and become steeper as training proceeds (Blough, 1969, 1975; Guttman & Kalish, 1956; Hearst, 1969; Heinemann & Rudolph, 1963; Rilling & Budnik, 1975; Sidman, 1961; see also Honig & Urcuioli, 1981; Rilling, 1977, for reviews). Theoretically, Gaussian distribution functions similar to those shown in Figure 2 provide the best approximations of empirical excitatory and inhibitory gradients (Blough, 1969; Ghirlanda & Enquist, 2003; Rilling, 1977). Although excitatory gradients have generally

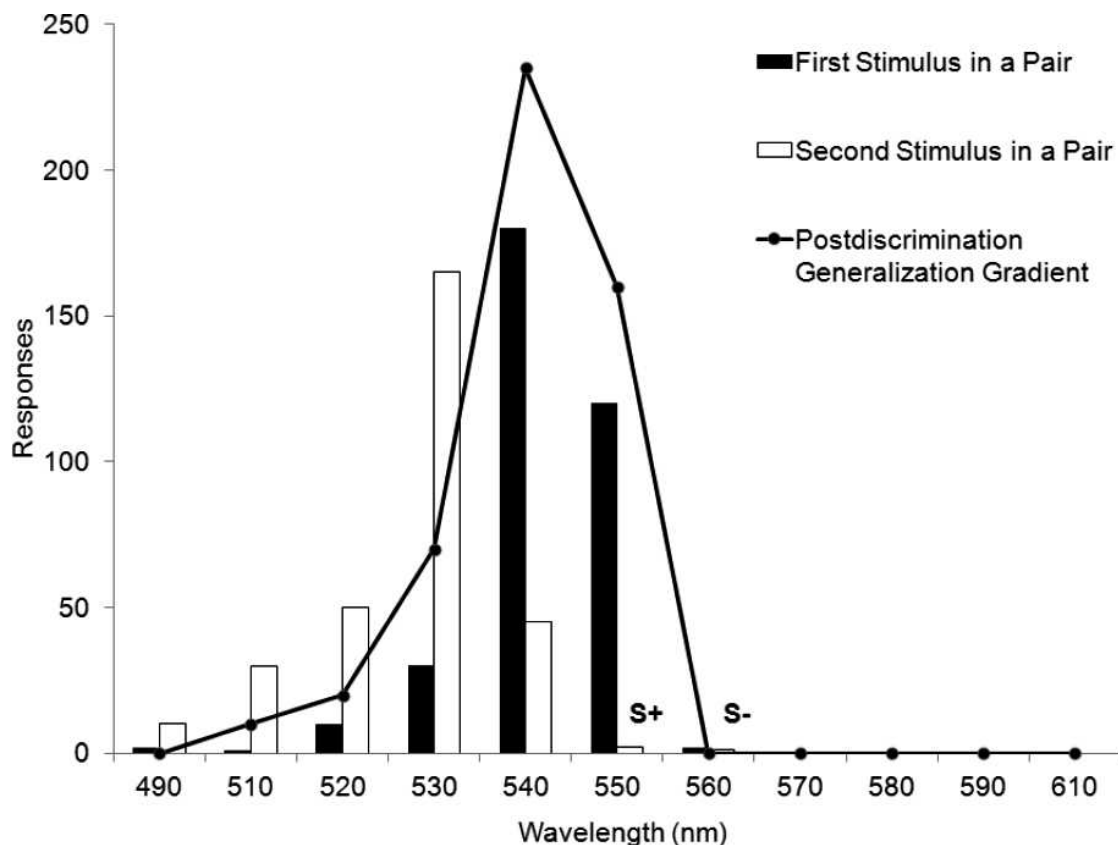


Fig. 3. A postdiscrimination generalization gradient obtained after successive discrimination training with S+ and S- (full line) and the choice preference (bars) for each consecutive pair (e.g., 490 vs. 510, 510 vs. 520, and so on). Note that the postdiscrimination generalization gradient shows clear peak shift away from S-, and a corresponding "relational" choice when 540 and 530 nm are paired, as well as transposition breakdown when 530 and 540 nm are paired. Redrawn from Honig, W. K. (1962).

been found to be taller and narrower than inhibitory gradients, some research suggested that these differences may be due to dissimilar procedures used to obtain these gradients and to disparities in measurement techniques (Jenkins, 1965). When the equivalent procedures are used, both excitatory and inhibitory gradients appear to have comparable shape (Honig, Boneau, Burstein, & Pennypacker, 1963); some reports have even found inhibitory gradients that are taller and narrower than excitatory gradients (Blough, 1975).

What about the PDG? Because the inhibitory gradient is subtracted from the excitatory gradient, it seems obvious that the excitatory gradient should be taller than the resulting PDG. The PDG should also be steeper between S+ and S- than an excitatory gradient and it should show a peak shift away from S-.

Figure 4 shows empirical verification of these predictions obtained by Hanson (1959). In this study, four experimental groups of pigeons were trained with the same S+ (550 nm) and one of the four possible S- (555, 560, 570, and 590 nm); a control group was trained with S+ alone. As Figure 4 clearly illustrates, all PDGs were steeper and taller than the control gradient, and they also showed a positive peak shift. Thus, Hanson's study provided a clear confirmation of two out of three predictions. Other research has also documented a *negative peak shift*, or a shift of a minimum of responding from S- in a direction away from S+ (Blough, 1975). The peak shift has been observed using different stimulus dimensions and in different species (Cheng & Spetch, 2002; Cheng, Spetch, & Johnston, 1997; Derenne, 2006; Ghirlanda & Enquist, 2003;

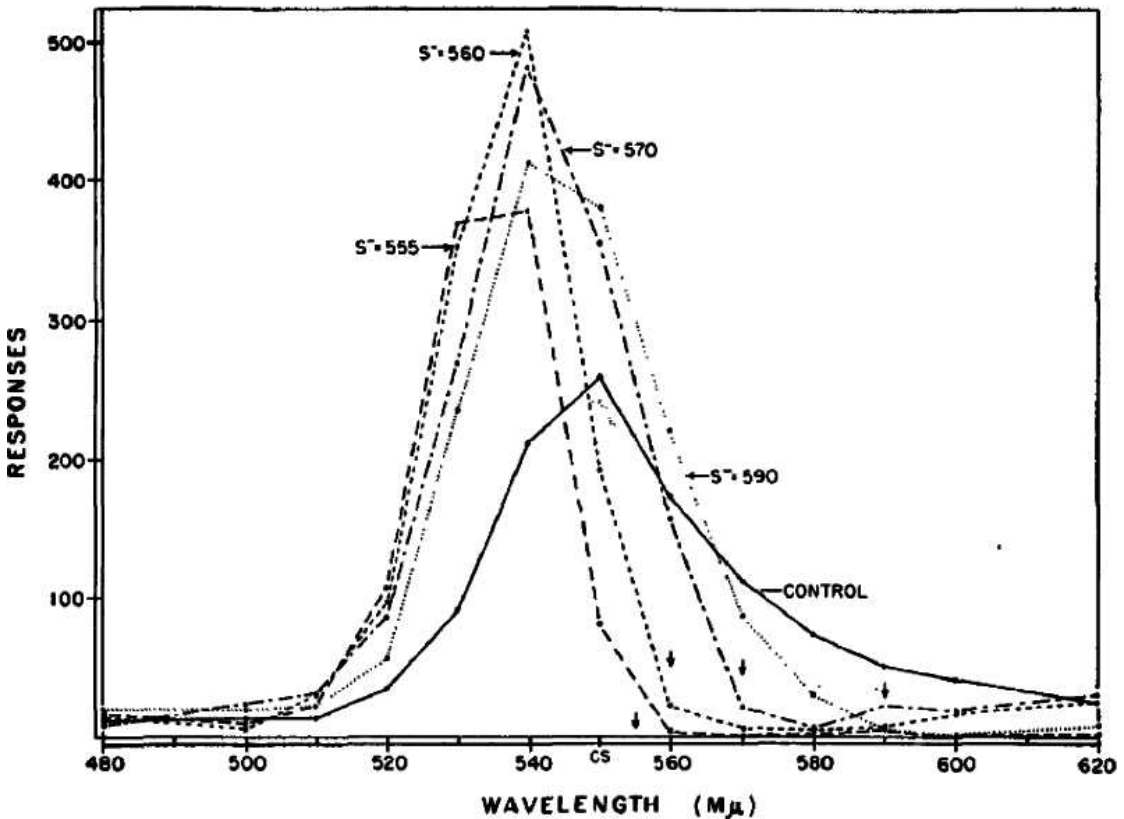


Fig. 4. Mean generalization gradients obtained after training with 550 nm as S+ and one of the four S- values shown on each gradient. The control group was trained with 550 nm as S+ only. Note that while the peak of responses is located at S+ for the control group, it is shifted away from S- for each of the four experimental groups. From Hanson, H. M. (1959).

Purtle, 1973; Spetch, Cheng, & Clifford, 2004; Wisniewski, Church, & Mercado, 2009). Similarly, *behavioral contrast* (a taller PDG in comparison to a corresponding excitatory gradient) has been consistently found in multiple studies (reviewed by Freeman, 1971; Purtle, 1973).

Do all discrimination training procedures in which S+ and S- are located on the same dimension produce a peak shift? Research suggests that the answer is no. Extensive amounts of training can reduce or even completely eliminate a peak shift (Gerry, 1971; Migler & Millenson, 1969; Terrace, 1966). The spacing of S+ and S- also affect a peak shift (cf. Figure 4): The S+ and S- that are close to each other on a sensory dimension are more likely to produce a peak shift, while distant S+ and S- may fail to produce a peak shift altogether (Derenne, 2006; Hanson, 1959; Thomas, 1962; Thomas, Mood, Morrison,

& Wiertelak, 1991). Theoretically, the slope of the inhibitory gradient between S+ and a new stimulus must be steeper than the slope of the excitatory gradient in order for the positive peak shift to occur; the opposite is true for the negative peak shift (Rilling, 1977, pp. 448–449). Therefore, excitatory and inhibitory gradients spaced far on a sensory dimension will fail to produce a peak shift as will the closely spaced gradients that are steepened due to extensive discrimination training. Figure 5 illustrates this idea using theoretical excitatory and inhibitory gradients. The same gradients that produced a strong peak shift shown in Figure 2 fail to produce any noticeable peak shift when the distance between the S+ and S- is tripled (Figure 5A), and consequently fail to predict transposition in the pair S2–S3. Figure 5B uses the same gradient spacing as shown in Figure 2 but employs narrower excitatory and inhibitory gradients; again, these gradients do not pro-

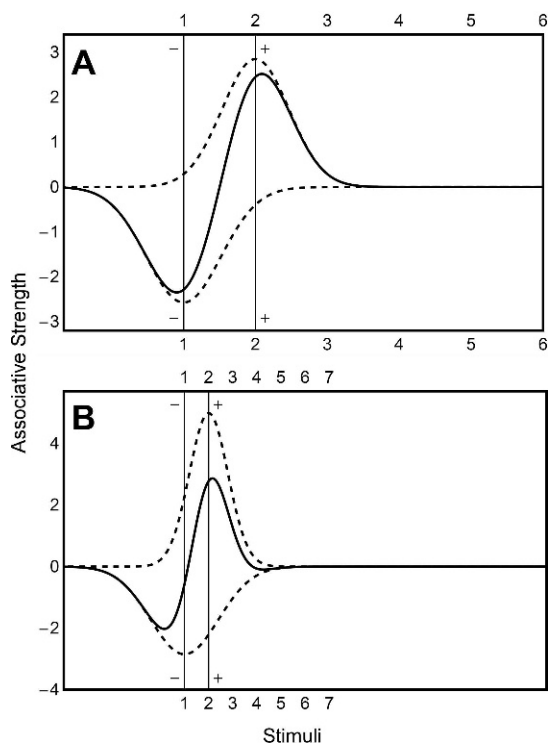


Fig. 5. Hypothetical excitatory and inhibitory gradients (dashed lines) and postdiscrimination generalization gradient (full line) illustrating the relationship between stimulus spacing (A), the width of excitatory and inhibitory gradients (B), and peak shift.

duce any peak shift and do not predict transposition in a pair S2–S3.

Figure 5 illustrates another important observation: the PDG does not always predict transposition for the near testing pair, because this prediction is affected by the spacing of the stimuli and the shape of the gradients. For example, in a recent study (Manabe, Murata, Kawashima, Asahina, & Okutsu, 2009) African penguins were trained to select either the shorter or the longer of the two lines (S2 of 2,000 pixels in length and S3 of 4,000 pixels in length). After the birds reached at least 90% accuracy, they were presented with two novel near test pairs: S1–S2 and S3–S4 (where S1 was 1,332 pixels and S4 was 6,000 pixels). At a glance, it appears that the PDG should predict relational choices in both of these near test pairs. However, as Figure 6 illustrates, S+ and S– in this experiment are separated by a considerable distance. The degree of spread of theoretical excitatory and inhibitory gradients

in these and other simulations is limited by the necessity to support high discriminative performance to the training pairs¹. The resulting theoretical PDG depicted in Figure 6 lacks a peak shift and, in fact, predicts strong absolute choices in both testing pairs, instead of the strong preference for the “relationally correct” stimulus reported in the study (an average of 82%).

Other Attempts to Explain Behavior in Transposition Experiments: Adaptation Level Theory

In its most general form, adaptation level theory (Helson, 1964) states that our perception of any object property is determined by both the current value of that property and by the previously experienced values, just like the sensitivity to light upon entering a dark room is a function of the present level of illumination and the level of illumination in a previous environment. Applying this approach to transposition, James (1953) proposed that during initial discrimination training an organism learns to select stimuli above a certain *adaptation level* and avoid stimuli below that level. Importantly, reinforcement and nonreinforcement affect which side of the adaptation level will be preferred, but have no effect on the actual location of that level. If two stimuli in a novel testing pair fall on each side of the adaptation level, then an organism will respond relationally. If the stimuli are located on the same side of the adaptation level, then an organism will respond at chance level. James also proposed that adaptation level is determined by a weighted geometric mean of current stimulus values and previous stimulus values:

¹Requiring that the combination of excitatory and inhibitory gradients predict high discriminatory performance in training pair(s) places tight constraints on the family of Gaussian distribution functions. Although multiple combinations can satisfy this requirement, they usually predict similar outcome in novel testing pairs (see Lazareva, Wasserman, & Young, 2005, Figures 3 and 4, and Table 1). Moreover, our prior attempts to find the best-fitting combination of excitatory and inhibitory gradients that simultaneously predict high discriminatory performance in training pairs and transposition novel testing pairs produced highly unrealistic excitatory and inhibitory gradients (Lazareva et al., 2005, p. 30–32), suggesting that preliminary simulations using Gaussian distribution functions can serve as a good initial estimate of the extent to which theoretical PDG can predict transposition in novel pairs.

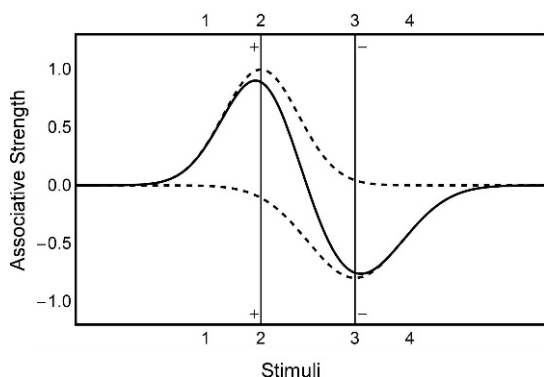


Fig. 6. Hypothetical excitatory and inhibitory gradients (dashed lines) and postdiscrimination generalization gradient (full line) for birds trained to select the smaller of the two lines in Manabe et al.'s (2009) experiment. Training to select the larger of the two lines results in similar predictions.

$$\log(AL) = c \frac{\sum \log X}{n_X} + p \frac{\sum \log Y}{n_Y} \quad (1)$$

where AL is adaptation level, c and p are relative weights given to testing and training stimuli, X and Y are the values of testing and training stimuli, and n_X and n_Y are the number of training and testing stimuli.

Note that if $c = 1$ and $p = 0$, then the adaptation level is determined exclusively by the testing stimuli and the subjects will demonstrate perfect transposition. As p increases, the likelihood of making a "relational" choice decreases. The factors that affect relative weights of testing and training stimuli are then of critical importance to the adaptation level account of transposition. Unfortunately, these factors have not been studied comprehensively. In addition, recent research suggests that the adaptation level approach does not easily apply to multiple-pair discrimination designs described below (Johnson & Zara, 1960; Lazareva et al., 2008; Lazareva et al., 2005; Marsh, 1967). For example, in one of our studies the pigeons were trained to discriminate S1 versus S2 and S5 versus S6 (Lazareva et al., 2005). According to adaptation level theory, this training ought to produce a single adaptation level between S2 and S5. However, this adaptation level cannot explain pigeons' ability to select the smallest stimulus in each of the training pairs, as S1 and S2 each fall on the low side of the

adaptation level and S5 and S6 each fall on the high side of adaptation level. One might assume that S1 versus S2 and S5 versus S6 training produce two adaptation levels, one between S1 and S2 and the other between S5 and S6. Still, it is not clear how these two levels interact to predict a choice of a stimulus in a testing pair S0 versus S7, where S0 falls below and S7 falls above both adaptation levels; or S3 versus S4, where S3 and S4 each fall above and below the two different adaptation levels. The situation becomes even more complex when three or more training pairs are used (cf. Figures 8 and 10). In short, adaptation level theory in its current state is unlikely to provide a comprehensive theoretical account of an organism's behavior in transposition experiments.

MULTIPLE-PAIR TRANSPOSITION DESIGNS

Prior Research Using Multiple-Pair Design

Most of the transposition research used a single training pair followed by a near test pair and one or more far test pairs. Johnson and Zara (1960) were first to point out that after a single-pair training either relational or absolute solution is "correct" since neither of them is emphasized by the training. In contrast, when two training pairs are employed, the relation among the items becomes a more economic solution as it can be used across both pairs.

Johnson and Zara (1960) trained 4-year-old children to simultaneously discriminate black squares of different sizes. In the first group, the children received a single simultaneous discrimination, S3–S4+ (where the smallest square, S1, was 1.6 in², with a constant increase ratio of 0.62). In the second group, they were trained with two pairs, S1–S2+ and S3–S4+. All children were then tested with S4–S5 (a near pair), S5–S6 and S6–S7 (two far pairs). As Figure 7 illustrates, children trained with a single pair showed a decline in transposition from the near pair to the far pairs, whereas children trained with two pairs showed nearly perfect transposition in all pairs. Johnson and Zara suggested that it would be impossible to find excitatory and inhibitory functions that simultaneously predict the decline in responses after one-pair training and no decline after two-pair training. Similar results were reported by Sherman and Strunk (1964) (also see

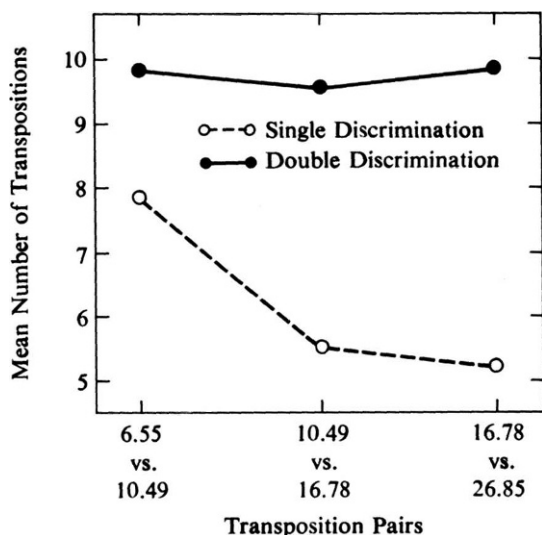


Fig. 7. Mean number of relational choices in 10 testing trials following a one-pair or two-pair training in Johnson and Zara's (1960) study. From Johnson and Zara (1960).

the review by Reese, 1968, pp. 67–80). Most importantly, it appeared that multiple-pair training enhanced transposition.

What about animals? In an elegant experiment, Marsh (1967) trained pigeons to discriminate different wavelengths (S1 of 520 nm, S2 of 540 nm, S3 of 550 nm, and S4 of 560 nm). The relational group of pigeons was trained with S1+ S2– and S3+ S4–, whereas the absolute group was trained with S1–S2+ and S3+ S4–. In other words, the first group received training emphasizing relational information, while the second group had to rely on absolute properties of the stimuli to learn both discriminations². In addition, the relational group comprised birds receiving simultaneous discrimination training that afforded a direct comparison of two stimuli, and a successive discrimination training that did not provide

such opportunity. In the test, all birds were given a single testing pair, S2–S3. Note that pigeons in the relational group ought to select the shorter of the two wavelengths; however, S2 had been previously not reinforced and S3 had been previously reinforced. Marsh reported that the relational group trained simultaneously selected S2 in a pair S2–S3 an average of 76% of the time, whereas the relational group trained successively preferred S2 only 41% of the time. Pigeons in the absolute group showed no significant preference (an average of 52% of S2 choices), an expected result since both S2 and S3 for this group were previously reinforced. This experiment suggested that simultaneous two-pair training produces relational responding that is strong enough to overcome reinforcement history of the stimuli. Unfortunately, these results have had very little effect on the perceived success of Spence's (1937) discrimination theory as an account of transposition (cf. Mackintosh, 1974; Riley, 1968; Rilling, 1977).

Research Using Multiple-Pair Designs

Empirical findings. In an initial study (Lazarova et al., 2005), we used circle size as a dimension to train three groups of pigeons to discriminate a single pair (S1–S2 or S5–S6), two pairs (S1–S2 and S5–S6), or four pairs of stimuli (S1–S2, S1–S3, S5–S6, and S4–S6). Figure 8 illustrates the design of this experiment (top panel) together with the theoretical PDGs for each training condition (bottom panel). In this and all other experiments the choice of the smaller or larger circle was counterbalanced across birds, but here I will only provide simulations for the condition in which the smaller circle was reinforced to simplify the description.

Note that our multiple-pair training is recognizably different from the training employed in earlier research. Both Johnson and Zara (1960) and Marsh (1967) used training pairs located next to each other on a sensory dimension. In contrast, our two-pair training included two training pairs separated by neutral stimuli, S3 and S4. This approach afforded us an opportunity to evaluate pigeons' responses to the novel testing pair S3–S4. As Figure 8 demonstrates, after two-pair training in which a smaller circle was reinforced, S4's nearest neighbor is a former S+ (S5) whereas S3's nearest neighbor is a former

²Although it may appear unlikely that an organism is able to discern the ordering of the colors along the spectral dimension, psychophysical research shows that this indeed is the case. Geometrically, perception of color similarity in pigeons is best described by a circular configuration, a color circle (Riggs, Blough, & Schafer, 1972; Schneider, 1972), just as in humans. Moreover, other behavioral research shows that pigeons can indeed discriminate shorter wavelengths from longer wavelengths (e.g., Blough, 1996). It is not clear, however, whether the stimuli in Marsh's (1967) experiment were controlled for brightness, so it is possible that this discrimination was based on brightness rather than true wavelength.

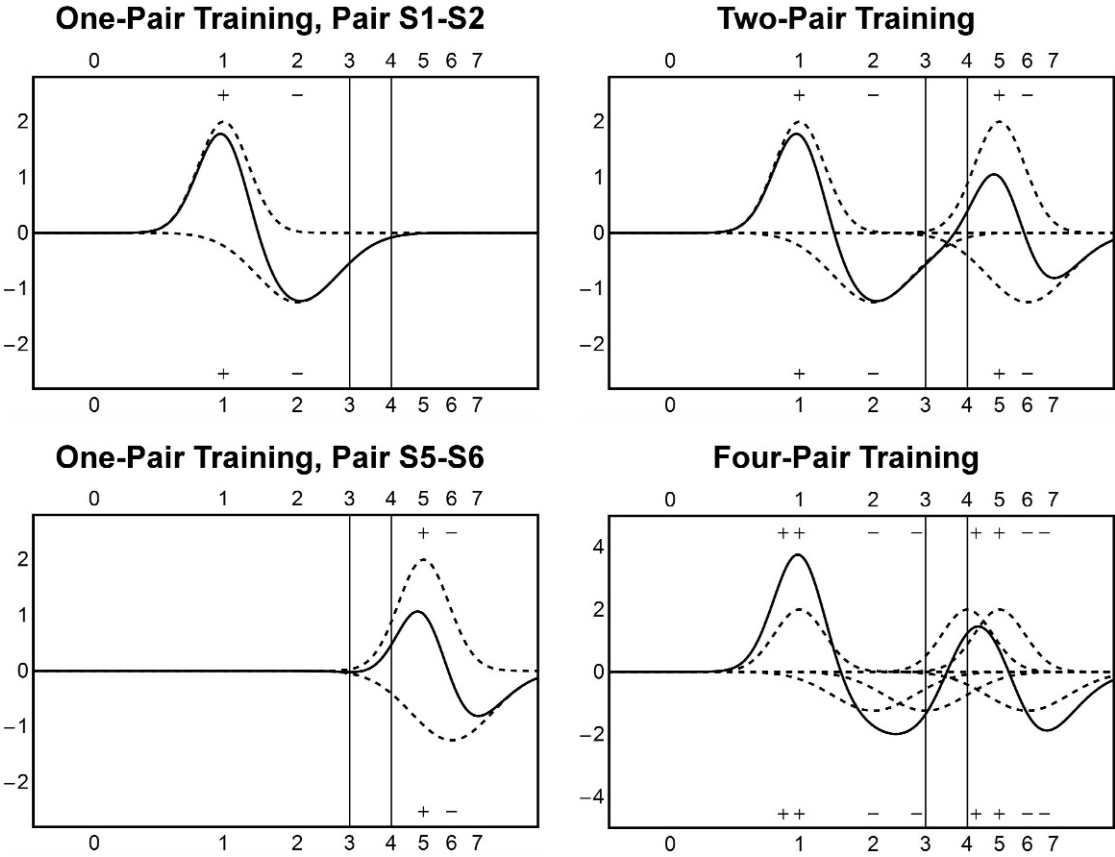
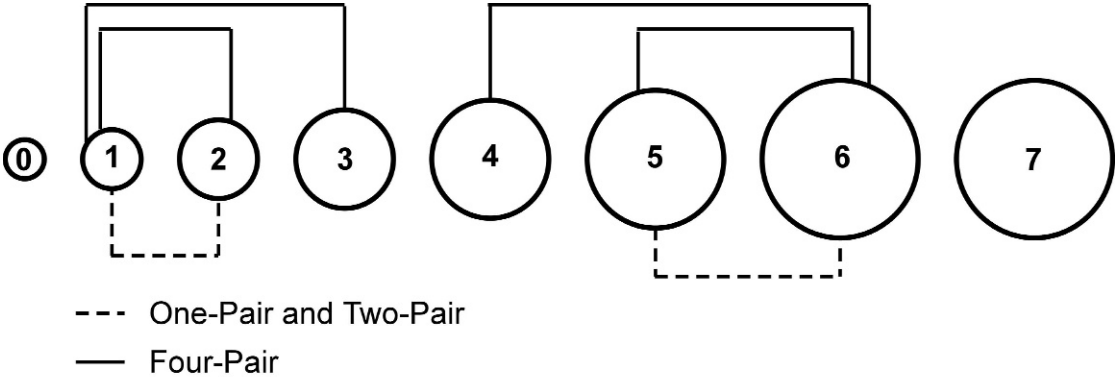


Fig. 8. A schematic representation of the experimental design employed in Lazareva et al. (2005), together with predicted postdiscrimination generalization gradients (solid lines) obtained by summation of excitatory and inhibitory gradients (dashed lines) after one-pair, two-pair, and four-pair training. The gradients are shown only for the condition in which the choice of the smaller circle was reinforced.

S– (S2). As in previous figures, the dashed lines are hypothetical excitatory and inhibitory gradients that resulted from the reinforcement or nonreinforcement of each stimulus

used in training. The PDG (solid line) predicts a choice of “relationally incorrect” S4 in a pair S3–S4. The PDG after four-pair training predicts very strong “absolute” choice of S4

as S4 is now a former S+ and S3 is a former S−. Yet, pigeons reliably selected S3 in a pair S3–S4 (an average of 58% after two-pair training and 70.7% after four-pair training).

Although most of the prior research used testing pairs that consisted of two stimuli located next to each other on a sensory dimension, our design employed a rich set of testing pairs with varying separation among the testing stimuli (i.e., S3–S4, S2–S3, S2–S6, and so on). Thanks to this diverse set of testing pairs, we found that the PDGs predicted unexpected relational choices even after one-pair training. For example, as Figure 8 illustrates, the PDG after one-pair training with the S1–S2 pair shows lower associative strength for S2 in comparison to stimuli S3 and S4. Consequently, the PDG predicts the choice of S3 in a pair S2–S3 and the choice of S6 in a pair S2–S6 even though the pigeons were trained to select the smaller of the two circles. Yet, the pigeons exhibited reliable relational behavior in both pairs selecting S2 over S3 and S2 over S6, or vice versa in a different counterbalancing (an average of 72.3% and 71.2%, correspondingly).

The diverse set of testing pairs also afforded an opportunity to evaluate the effect of spacing of the testing stimuli on pigeons' behavior. We found that the testing stimuli located far apart from each other on a dimension (e.g., S0–S7) engendered stronger relational responses than the testing stimuli located closer to each other (e.g., S3–S4), suggesting that highly dissimilar testing stimuli support more robust relational behavior.

Finally, we found that, on average, the proportion of relational responses increased from one-pair to two-pair to three-pair training (Figure 9A). However, this increase was, to some extent, captured by Spence's (1937) discrimination theory. With more excitatory and inhibitory generalization gradients interacting along size dimension (cf. Figure 8) there was a greater likelihood of predicting relational choices in any testing pair. Therefore, it was possible that the rise in proportion of relational choices after multiple-pair training was feasible only when the PDGs predicted the same outcome. To test this possibility, we designed a new experiment in which these two accounts gave opposite predictions (Lazareva et al., 2008).

Figure 10 illustrates the design of this experiment (top panel), as well as predictions

produced by the theoretical PDGs for each training condition (bottom panel). In the small circle condition, one-pair training involved S1–S2 discrimination, two-pair training involved S1–S2 and S2–S3 discrimination, and three-pair training involved S3–S4 discrimination. The critical testing pairs in this condition were S4–S5 and S5–S6. In the large circle condition the corresponding training involved S5–S6, S5–S6 plus S4–S5, and S5–S6, S4–S5, plus S3–S4 discriminations, and the critical testing pairs included S2–S3 and S1–S2.

As Figure 10 illustrates, the relationally correct stimuli (e.g., S4 in the pair S4–S5 and S2 in the pair S2–S3) gradually come closer to the former S− as the number of training pairs increases. After one-pair training, the PDGs predict chance performance as the testing stimuli are too far removed from the S+ and S− to acquire significant amount of generalized associative strength. After two-pair training, the “relationally correct” S4 in a testing pair S4–S5 becomes a nearest neighbor of a previously nonreinforced S3 in small circle condition; likewise, a “relationally incorrect” S3 in a testing pair S2–S3 becomes a nearest neighbor of a previously reinforced S3. Consequently, the PDGs predict the absolute choice in both of these pairs and a chance performance for two other pairs, S5–S6 in small circle condition and S1–S2 in large circle condition. Finally, after three-pair training the PDGs predict strong absolute choice in both testing pairs. In the small circle condition, the “relationally correct” S4 in the testing pair S4–S5 is now nonreinforced during training; likewise, in the large circle condition, the “relationally incorrect” S3 is now reinforced during training. In other words, the PDGs predict a *decrease* in proportion of relational choices with an increase in the number of training pairs. Yet, our pigeons, on average, again showed a reliable increase in transposition responses (Figure 9B; see also Figure 11 for predictions of PDGs for individual pairs in different conditions).

Theoretical considerations. Our research clearly demonstrated that multiple-pair training facilitates transposition even when PDGs predict an opposite outcome. However, this result does not imply that PDGs have no influence on pigeons' responses. On the contrary, our data (as well as an extensive body of prior research) indicates that PDGs produced by

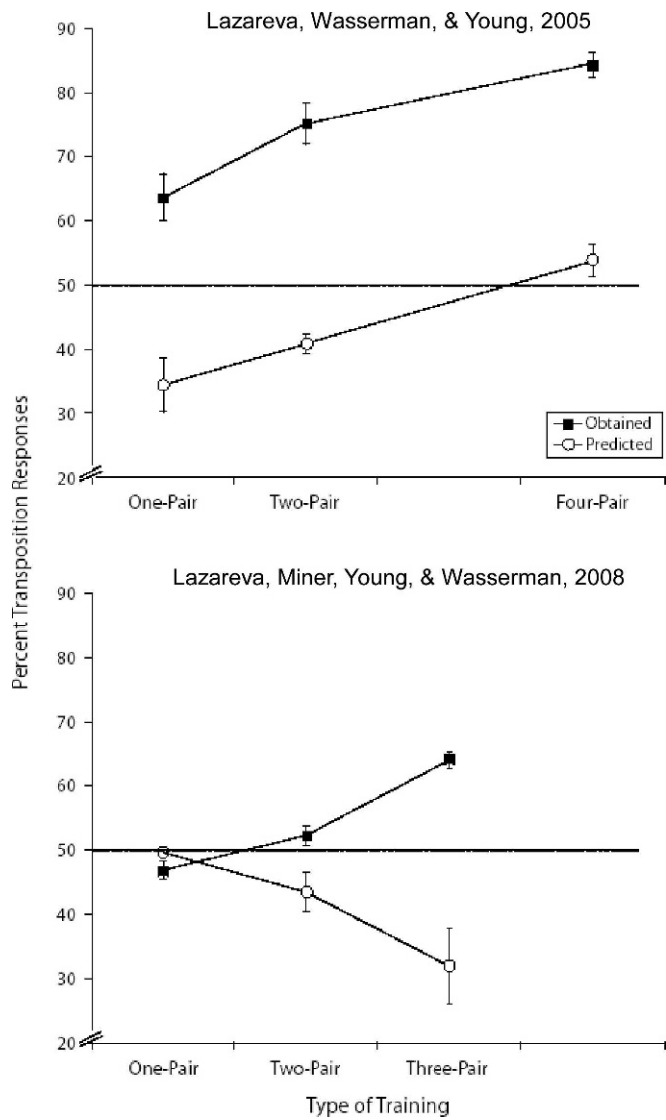


Fig. 9. Mean percentage of relational choices obtained after multiple-pair training and predicted by the hypothetical postdiscrimination stimulus generalization gradients based on Spence’s (1937) theory. The top panel (A) depicts data reported in Lazareva et al. (2005). The bottom panel (B) depicts data reported in Lazareva et al. (2008). From Lazareva et al. (2008).

prior training affect pigeons’ choices, although their influence may be relatively weak, especially after multiple-pair training. For example, after one-pair training with S1–S2 (cf. Figure 8) the PDG predicts a high proportion of relational choices in a pair S1–S5 and a high proportion of absolute choices in a pair S2–S6. Although the pigeons responded relationally in both pairs (Lazareva et al., 2005), the proportion of relational choices was significantly higher in the pair

S1–S5 (an average of 92.3%) than in the pair S2–S6 (an average of 71.3%) indicating a potential influence of PDG on birds’ performance. The second parameter that exerts strong influence on pigeons’ behavior is the degree of similarity between two stimuli in a testing pair. Unlike PDG, this parameter is relational in nature and reflects the intuition that the more similar two stimuli are to each other, the more difficult it is to determine which of them

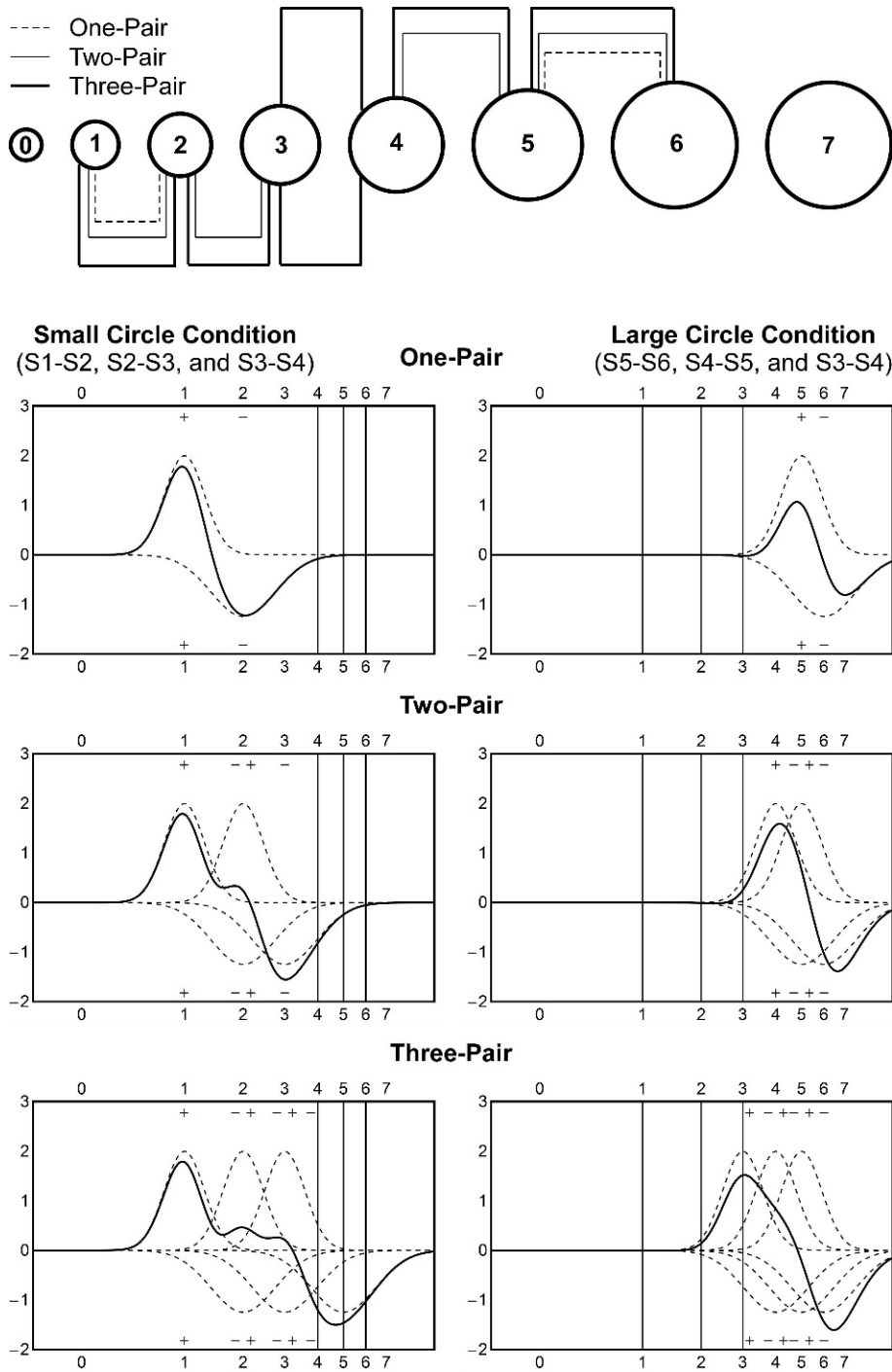


Fig. 10. A schematic representation of the experimental design employed in Lazareva, Miner, Wasserman, and Young (2008), together with postdiscrimination generalization gradients (solid lines) obtained by summation of excitatory and inhibitory gradients (dashed lines) after one-pair, two-pair, and three-pair training. The gradients are shown only for the condition in which the choice of the smaller circle was reinforced.

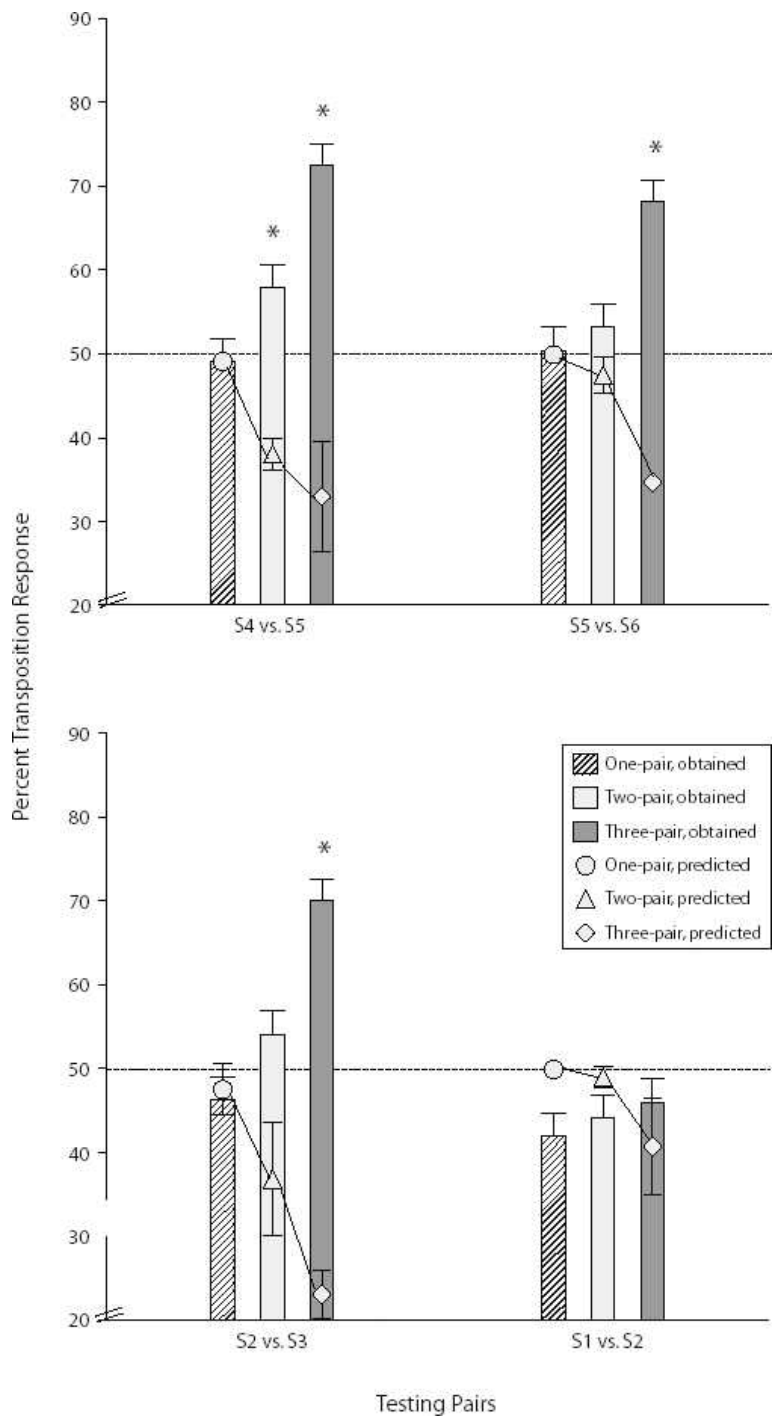


Fig. 11. Mean percentage of relational choices obtained to testing pairs and predicted by the hypothetical postdiscrimination stimulus generalization gradients shown in Figure 10 after training with S1–S2, S2–S3, and S3–S4 (A) or with S5–S6, S4–S5, and S3–S4 (B). From Lazareva et al. (2008).

is larger (or brighter, faster, etc.) leading to poorer relational responding. We represented this parameter termed *relational disparity* by the scaling function

$$r = \log_2(y) - \log_2(x), \quad (2)$$

where r is the difference in scaled stimulus diameters, x is the diameter of the smaller testing circle, and y is the diameter of the larger testing circle. The function uses logarithmic rather than absolute values because constant differences in size are not equally discriminable (Peissig, Kirkpatrick-Steger, Young, Wasserman, & Biederman, 2006).

Note that large values of r correspond to the large difference between testing circles and are expected to produce more relational responses than smaller values of r . Our initial study (Lazareva et al., 2005) confirmed this expectation. However, our subsequent study (Lazareva et al., 2008) produced somewhat different results. As Figure 11A illustrates, in the small-circle condition the birds showed stronger relational responding in the testing pair S4–S5 ($r = 0.26$) than in the pair S5–S6 ($r = 0.22$). However, in the large-circle condition (Figure 11B), the birds showed stronger relational responding to the testing pair S2–S3 ($r = 0.42$) than to the pair S1–S2 ($r = 0.59$), contrary to the r values. It therefore appeared that another parameter was affecting relational responding in addition to PDG values and relational disparity.

We hypothesized that relational responding is also affected by the similarity of the testing configuration as a whole to the training configuration as a whole, a factor that we term *familiarity*. This parameter is again relational in nature and reflects the intuition that the more similar the testing situation is to the training situation, the more likely the organism is to deploy the particular strategy that was learned during training. The notion that overall similarity of the testing configuration to the training configuration affects the probability of relational responding dates back to Köhler who suggested that the perception of the relationship breaks down when the testing pairs are dramatically different from the training pairs (Köhler, 1929; see also Gulliksen & Wolfle, 1938; Riley, 1958; Stevenson & Bitterman, 1955, for a similar argument). To our knowledge, this idea has never been expressed quantitatively.

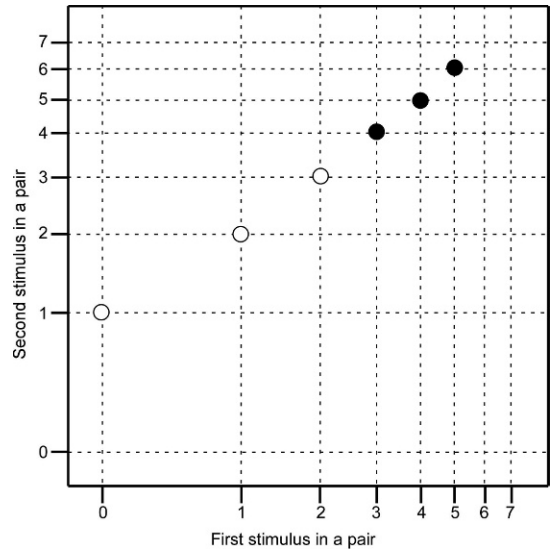


Fig. 12. Example of the hypothetical Euclidean distance space containing training pairs used in Lazareva et al. (2008).

We represented this parameter as the inverse of Euclidean distance from the testing pair to the *nearest* training pair in a log-scaled two-dimensional space:

$$f = 1 - d, \quad (3)$$

$$d = \sqrt{[\log_2 x - \log_2 y]^2 + [\log_2 a - \log_2 b]^2}, \quad (4)$$

where f is familiarity, d is the Euclidean distance, x and y are the diameters of the stimuli comprising a *testing pair*, and a and b are the diameters of the stimuli comprising the *nearest training pair*.

Figure 12 illustrates the Euclidean distance space for three-pair training. In the small-circle condition the birds were presented with the testing pairs S4–S5 and S5–S6, both of which are reasonably close to the nearest training pair S3–S4. In contrast, the testing pair S1–S2 presented to the birds in the large-circle condition is much farther away from the nearest training pair S3–S4. Consequently, the familiarity function predicts the most robust relational responding in the testing pair S4–S5 and the least robust relational responding in the pair S1–S2.

At first glance, the familiarity function may appear to be similar to stimulus generalization. After all, generalization of associative strength

is a function of the similarity of the training stimuli to the testing stimuli (Shepard, 1987), as testing stimuli located closer to the training stimuli acquire more associative strength than testing stimuli located farther away. However, to predict a choice in a testing pair using generalized associative strength one needs to consider whether the training stimulus was reinforced or nonreinforced during training. For example, the stimulus generalization approach predicts absolute choice in the pair S4–S5 after two-pair training with S1+ S2– and S2+ S3– because the relationally correct S4 is close to the previously nonreinforced S3 (cf. Figure 10). In contrast, the familiarity function does not take into account the reinforcement history of the training stimulus. Instead, it concentrates on overall similarity of the testing pair to the training pair predicting relational response in the pair S4–S5 as it is reasonably close to one of the training pairs.

How do these three parameters interact to predict pigeons' behavior in a transposition task? The limited set of testing pairs in our published studies does not allow a quantitative evaluation of the reliability of these functions as predictors of transposition at this time. It is clear, however, that all three functions—generalization of associative strength, relational disparity, and familiarity—modulate relational responses, and need to be taken into account to develop a comprehensive account of relational behavior in a transposition task.

CONCLUSION

Can animals respond to relations in a transposition task? Prior transposition research often produced data that did not provide clear support for either stimulus generalization theory or relational learning accounts. Multiple studies provided strong support for basic premises of Spence's (1937) generalization theory and its predictions, such as the shapes of PDGs and peak shifts (Ehrenfreund, 1952; Hanson, 1959; Hearst, 1969; Honig, 1962; Kalish & Guttman, 1959). On the other hand, some studies reported relational responding in a transposition task that would be difficult to explain by appealing solely to the generalization of associative strength from the training stimuli to the testing stimuli (Johnson & Zara, 1960; Lawrence & DeRivera, 1954; Marsh, 1967; Riley et al., 1960). Unfortunately, the strong

empirical evidence questioning generalized associative strength as a sole predictor of animals' behavior in a transposition task was not accompanied by a comparable development of alternative theoretical accounts.

Current research (Lazareva et al., 2008; Lazareva et al., 2005) provides strong evidence against generalization of associative strength as the sole determinant of transfer behavior in a transposition task. We showed that encountering multiple pairs of stimuli during training improves relational responding in the test even when reinforcement history predicts an opposite trend. Our data also suggest that an organism's behavior in a transposition test is affected by at least three factors—a generalized associative strength, a similarity of the two testing stimuli to one another, and the overall similarity of the testing pair to the training pair. Importantly, the two latter factors are relational in nature, suggesting that the animal might be learning both relational and absolute information during initial training. This proposal is in line with recent experimental evidence demonstrating simultaneous control by both absolute and relational properties of the stimuli in same-different discriminations and in categorization tasks (Bodily, Katz, & Wright, 2008; Gibson & Wasserman, 2003; Katz, Wright, & Bachevalier, 2002; Lazareva, Freiburger, & Wasserman, 2004).

In addition, our research emphasizes an importance of two experimental manipulations that need to be incorporated into future experiments—multiple pairs of training stimuli and a wide range of testing pairs that include nonadjacent testing stimuli. Our research shows that use of testing pairs composed of nonadjacent stimuli has the potential to uncover instances of relational learning even after one-pair training, and that multiple-pair training dramatically enhances control by the relation among the stimuli. I believe that this area is rich with new and unexpected findings despite the long and extensive history of research, and I hope that our efforts will renew the interest in relational learning associated with transposition.

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